

*ADELPHYDRAENA*, NEW GENUS, AND TWO NEW  
SPECIES FROM VENEZUELA, AND REMARKS  
ON PHYLOGENETIC RELATIONSHIPS WITHIN  
THE SUBTRIBE HYDRAENINA  
(COLEOPTERA: HYDRAENIDAE)

Philip D. Perkins

*Abstract.*—A new genus of aquatic beetle, *Adelphydraena* (Coleoptera: Hydraenidae) and two new species are described. The new species are from southern Venezuela: *A. spangleri* was collected from a stream at the base of the tepui Cerro de la Neblina; *A. orchymonti* was collected from a stream near Puerto Ayacucho. Synapotypic and plesiotypic character states of the genera *Adelphydraena* and *Hydraena* are discussed. Phylogenetic relationships within the genus *Hydraena*, and evolution of the lineage leading to *Hydraena* s.s. are also discussed. Taxonomically and phylogenetically significant structures of the two new species are illustrated.

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The sandstone mesas in northern South America, known locally as tepuis, have perhaps a greater concentration of floral and faunal endemics than any other area in the Americas. The tepuis are of great age, apparently having undergone relatively little of the massive geological and climatic changes which greatly modified South America after separation from Africa. Some of the endemic species found on or near the base of tepuis are thought to represent phylogenetically relictual taxa. The new genus *Adelphydraena* described below appears to be such a phylogenetic relict.

A biological survey of one of the tepui areas in Venezuela, Cerro de la Neblina Park, was conducted in 1985 by several institutions under the organization and direction of the Venezuelan Government (Spangler 1985). A team from the Smithsonian Institution, comprised of Paul J. Spangler, Phyllis M. Spangler, Robin A. Faitoute, and Warren E. Steiner, surveyed the aquatic insects. Collecting on the tepui and in streams near the base, the team collected over 55,000 insects, including a total of 16,694 specimens of aquatic Coleoptera, representing

many genera and families. Despite the remarkably high number of specimens, with collections from many habitat types, the material included only a single specimen of the new genus *Adelphydraena*.

In 1986, Paul J. Spangler collected aquatic insects near Puerto Ayacucho, which is about 400 miles north of Cerro de la Neblina Park. Among 2419 specimens of aquatic Coleoptera collected by Spangler was a second specimen, representing a second species, of *Adelphydraena*.

Members of the new genus *Adelphydraena* are phylogenetically revealing in that they retain several ancestral characteristics which are found in the derived state in the putative sister-group, the widespread and successful genus *Hydraena*. The combination of plesiotypic versus apotypic character states of members of *Adelphydraena* reveal part of the sequential development of derived characters in the lineage leading to *Hydraena* s.s.

Based on the extreme rarity of the specimens, and remoteness of the habitat, it seems unlikely that new material will soon be forthcoming. Therefore, the new genus

and two new species are described at this time.

*Adelphydraena*, new genus

*Type species.*—*Adelphydraena spangleri*, new species.

*Description.*—Form: Body oblong, elytra sometimes ovate. Size: Length 1.24–1.72 mm, width 0.58–0.84 mm. Color: Brown; pronotum lighter than head and elytra. Head: Frons with a low carina at rear, arcuate to posterior. Fronto-clypeal suture well developed. Labrum long, projecting anteriorly, with deep median emargination to form two lobes, each lobe approximately parallel sided; labrum not expanded on sides near base. Mentum long, sides slightly convergent from posterior to anterior; apicomedian emargination well developed. Maxillary palpi elongate, combined lengths of articles longer than ventral surface of head; ratios of articles 2, 3, and 4 (last) about 3:1:2. Antennomeres 10 (5+5) (Fig. 11). Mandibles with lateral surface visible in dorsal aspect; not interlocking with labrum. Pronotum: Sides produced, sometimes subcordiform, margin weakly denticulate. Disc with shallow transverse depression across base, lacking posterointernal foveolae; a weakly developed, incomplete transverse depression slightly anterior to midlength, depression slightly arcuate to posterior and interrupted in middle. Elytra: Nine complete rows of punctures, row ten reduced to a few punctures in anterior. Explanate margin moderate to well developed. Prosteronum: Intercoxal process broad, flat, expanded laterally behind coxae, coxal cavities closed; postcoxal process with a low carina on each side extended posteriorly from median margins of procoxae. A median longitudinal, low carina in front of coxae; carina extended beyond anterior margin to form very small apicomedian process. Anterior margin on each side of apicomedian process with small acute process slightly larger than apicomedian process. Trochan-

ter concealed. Proepisternum wide, not emarginate anteriorly, hence antennal cavities without ventral opening. Low carina separating hypomeron and proepisternum becoming effaced in anterior 0.33. Antennal cavities well developed. Mesosternum: Mesosternum with low median longitudinal carina and two carinae on each side, one carina at mesosternal-mesepisternal suture and one carina about midway between the latter and median carina. Sometimes with weakly developed carina extended anteriorly from each side of mesosternal intercoxal process. Mesosternal intercoxal process short, broad. Metasternum: Low median longitudinal carina in anterior 0.5. Plaque size and shape varying (Figs. 2, 3). Each side with two longitudinal low ridges or cuticular thickenings, visible when in fluid, one extended from middle of margin of mesocoxal cavity and one extended from near posterior limit of lateral carina of mesosternum. Abdomen: Intercoxal sternite slightly wider than mesosternal intercoxal process, fused with first sternum to form plate, plate delimited on each side by a low ridge extended posteriorly from median margin of metacoxal cavity. Suture between intercoxal sternite and first sternum visible through cuticle, sometimes not expressed externally. Legs: Tarsi with five articles. All femora moderately narrowed in basal 0.33. Ventral Vestiture: Vestiture extremely short and dense.

*Etymology.*—Greek *adelphē* (sister), plus *Hydraena*. *Adelphydraena* is the putative sister-group of *Hydraena*.

*Adelphydraena spangleri*, new species

*Type data.*—Venezuela, Territorio Federal Amazonas, Cerro de la Neblina, 1 km SE. Basecamp, 0°50'N., 66°10'W., 140 m, 21 Feb 1985, P. J. and P. M. Spangler, R. A. Faitoute, W. E. Steiner. Holotype female deposited in the National Museum of Natural History, Smithsonian Institution.

*Description.*—Size: Body 1.72 × 0.84

mm; pronotum  $0.40 \times 0.68$ ; elytra  $0.96 \times 0.84$ . Color: Brown-testaceous. Head: Frons finely punctate, punctures smaller than eye facets; shiny in middle, microreticulate and dull laterally; posterior line not extended forward at juncture of shiny and microreticulate areas. Clypeus strongly microreticulate. Labrum slightly longer than clypeus; median emargination setose, length nearly  $0.66 \times$  labrum length. Eyes small in dorsal aspect, width  $0.3 \times$  interocular distance. Mentum elongate, narrowed anteriorly, lobe on each side of apicomedian emargination curved ventrally and toward midline; apical width  $0.5 \times$  basal width. Genae without posterior ridge. Pronotum: Pronotum subcordiform. Posterior 0.5 of disc with raised, rounded relief on each side of midline, reliefs separated anteriorly by two large punctures side-by-side, followed by a single puncture in midline; reliefs very shiny, very finely, sparsely punctate, punctures similar to those of frons. Punctures posterior to reliefs very coarse and dense, forming two transverse rows, rows separated from one another by confluent interstices which form transverse line slightly less raised than discal reliefs, transverse raised line connected to each discal relief by similarly raised, short longitudinal line on each side of midline. Punctures anterior to discal reliefs coarse, slightly smaller than posterior punctures, shallow, bottoms apparently flat with central seta, interstices shiny,  $0.51-1.0 \times$  puncture diameter. All interstices anterior and posterior to discal reliefs with extremely sparse, very fine punctures similar in size to those of discal reliefs. Lateral depressions with punctures less developed and interstices less shiny than punctate discal areas. Lateral margin denticulate, more distinctly so anterior to middle. Anterior margin weakly trisinate. Posterior margin weakly bisinate. Elytra: Punctures on disc  $1 \times$  punctures on anterior area of pronotal disc. Intervals raised slightly, shiny,  $2-3 \times$  puncture diameter. Punctures in anterior 0.5 of rows 1-5 larger and more widely spaced than on

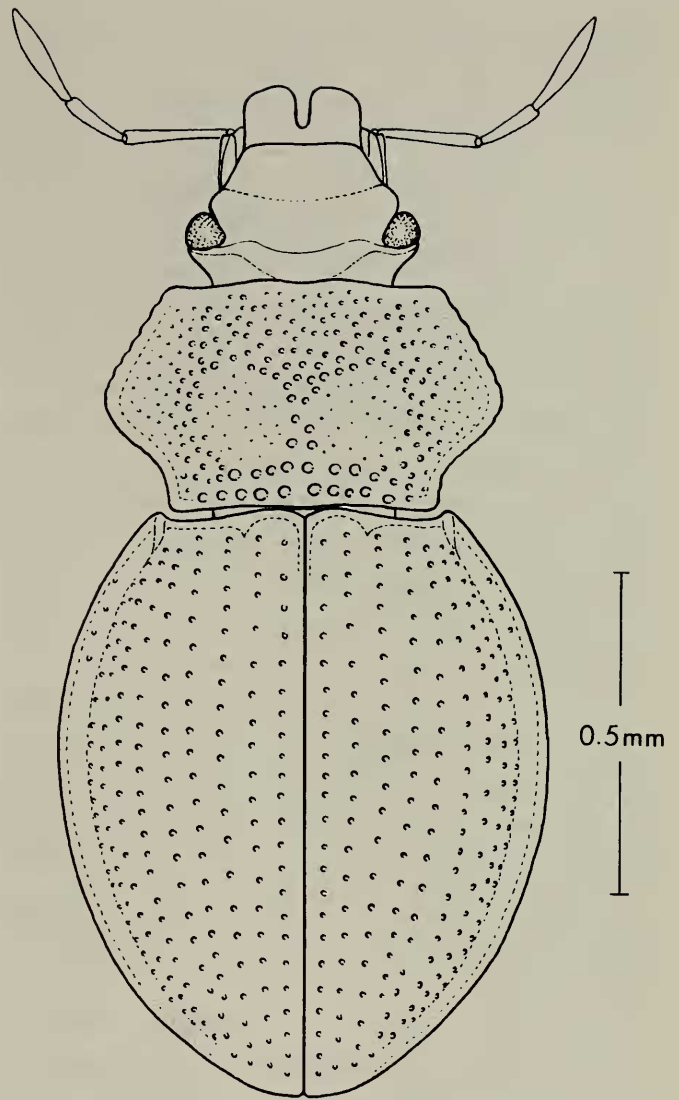


Fig. 1. *Adelphydraena spangleri*, new species, habitus.

remainder of elytron, interstices  $2-4 \times$  puncture diameter. Raised humeri connected with slightly produced anterior angles. Lateral margin strongly arcuate, explanate margin well developed, at midlength slightly wider than distal width of metatibia. Anterior margin with extremely small, posteriorly produced acute process at base of second interval. Prosternum: Prosternal intercoxal process as wide as mesosternal intercoxal process; prosternal midline length  $2.75 \times$  prosternal intercoxal process width. Prosternal postcoxal process flat between submedian carinae. Mesosternum: Mesosternal intercoxal process length  $1 \times$  width, apex slightly arcuate. Submedian carinae attaining thickened anterior border of meta-

sternum. Metasternum: Plaques well developed (Fig. 2). When in fluid, a dark longitudinal line of strength visible, extended posteriorly from each mesosternal suture to near posterior margin of metasternum. Abdomen: Distance separating coxal cavities  $2 \times$  mesosternal intercoxal process width. Submedian carinae of first sternum terminated slightly before posterior border of first sternum, distance separating carinae at posterior extreme slightly greater than midline length of first sternum plus fused intercoxal sternite. Sterna 1–5 with hydrofuge, sterna 6 and 7 shiny, sparsely pubescent. Legs: All legs without apparent modifications. Flight wings: Fully developed. Spermatheca: Fig. 13 (male unknown).

*Habitat.*—The holotype was seined from rocks and leaf packs in the rapids of a white-water stream. The stream was 5 m wide and 30 cm deep, with sand/gravel margins and bottom; oxygen, 9 ppm; hardness, 0; pH, 5.0; water temperature 29°C. The air temperature was a sweltering 42°C (Spangler, pers. comm.).

*Etymology.*—It is with pleasure that I dedicate this new species to Paul J. Spangler, whose dynamic fieldwork has provided a wealth of aquatic Coleoptera for systematic studies.

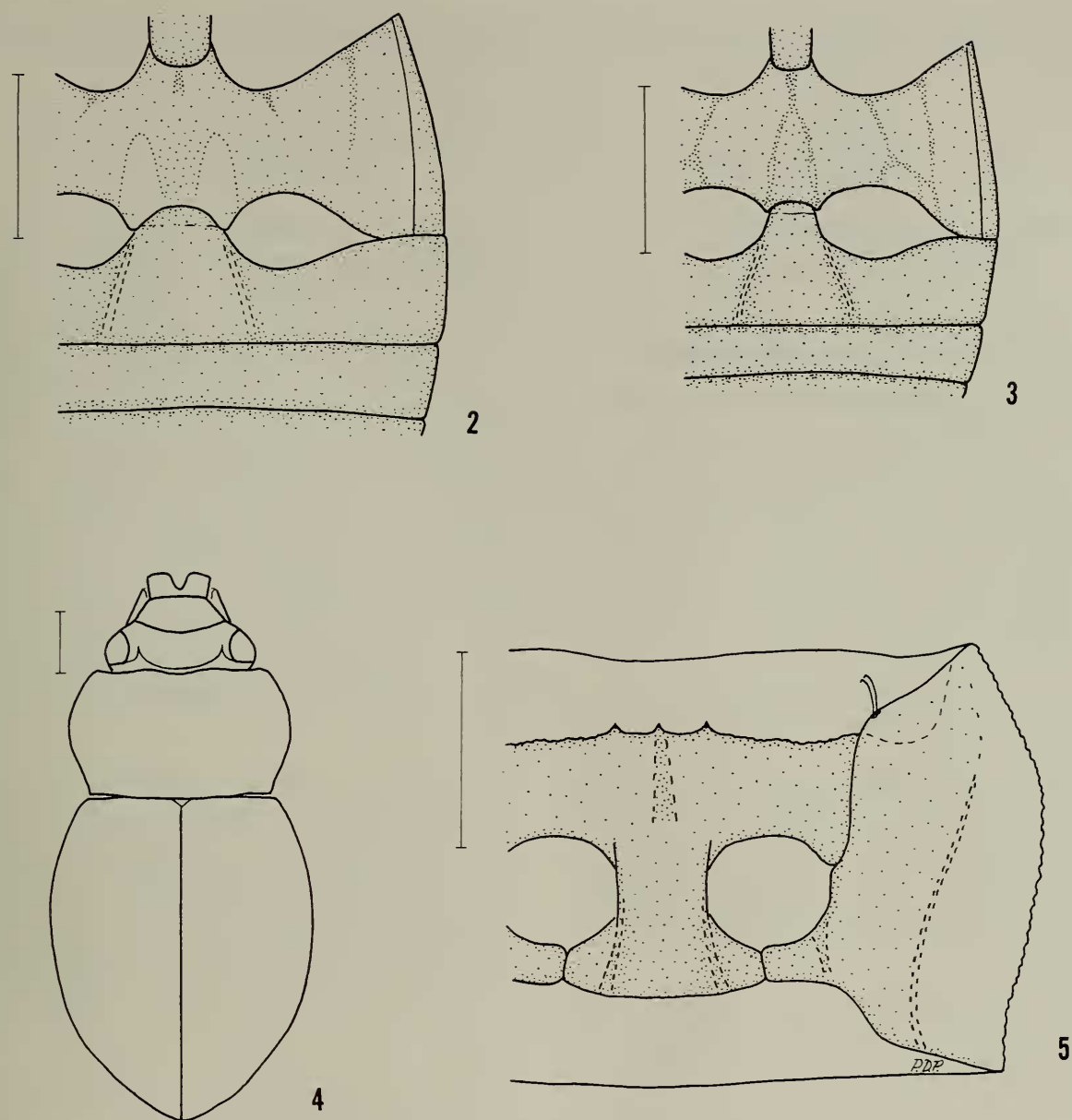
*Adelphydraena orchymonti*, new species

*Type data.*—Venezuela, Territorio Federal Amazonas, Puerto Ayacucho (40 km S.) at Tobogán, 24 Feb 1986, P. J. Spangler. Holotype female deposited in the National Museum of Natural History, Smithsonian Institution.

*Diagnosis.*—*Adelphydraena orchymonti* and *A. spangleri* differ markedly in many characteristics. *A. orchymonti* lacks the subcordiform shape of the pronotum and broadly explanate elytra seen in *A. spangleri* (Figs. 1, 4), and is much smaller, 1.24 vs. 1.72 mm. The metasternal plaques are very small in *A. orchymonti* and very large in *A. spangleri* (Figs. 2, 3). The shape of the men-

tum differs in the two species (Figs. 9, 10). Additional differences detailed in the species descriptions include sculpture of the pronotum and head, relative widths of elytral punctures and intervals, and relative widths of the intercoxal processes.

*Description.*—Size: Body  $1.24 \times 0.58$ ; pronotum  $0.32 \times 0.54$ ; elytra  $0.76 \times 0.58$ . Color: Brown, pronotum lighter than head and elytra. Head: Frons finely punctate, punctures smaller than eye facets; posterior arcuate line with lateral area extended forward. Clypeus finely punctate. Labrum as long as clypeus; median emargination setose, length slightly greater than  $0.5 \times$  labrum length. Eyes small in dorsal aspect, width  $0.2 \times$  interocular distance. Genae without posterior ridge. Pronotum: Disc with two slightly depressed, transverse areas with large, well impressed punctures  $4\text{--}5 \times$  eye facets, separated by thin walls: one area occupying basal 0.25 of disc, other area an ill-defined line, arcuate to posterior, across disc slightly anterior to middle; relief between coarsely punctate areas very finely, sparsely punctate, punctures  $1 \times$  frons punctures, interstices shiny; area anterior to transverse line of coarse punctures with punctures becoming increasingly smaller toward anterior, those at margin  $1 \times$  frons punctures. Lateral depression finely sparsely punctate, moderately produced slightly anterior to midlength. Elytra: Punctures on disc  $1 \times$  largest pronotal punctures. Intervals raised slightly, shiny,  $1 \times$  puncture diameter on disc, slightly narrower at intervals 4–6. Interstices slightly less than  $1 \times$  puncture diameter. Anterior margin with extremely small, posteriorly produced acute process at base of second interval. Prosteronum: Prosternal intercoxal process as wide as mesosternal intercoxal process; prosternal midline length  $2.66 \times$  prosternal intercoxal process width. Prosternal postcoxal process slightly concave between submedian ridges (Fig. 5). Mesosternum: Mesosternal intercoxal process length  $0.66 \times$  width, apex slightly rounded. Submedian



Figs. 2-5. 2, *Adelphydraena spangleri*, metasternum and anterior abdominal sterna; 3, *A. orchymonti*, same; 4, *A. orchymonti*, body outline; 5, *A. orchymonti*, prosternum. (Scale lines equal 0.1 mm.)

carinae not attaining thickened anterior border of mesosternum. Metasternum: Plaques extremely small, located at border of median, triangular, shallow depression. Apex of triangular depression joining low median carina to form inverted Y (Fig. 3). Abdomen: Distance separating coxal cavities  $1.25 \times$  mesosternal intercoxal process width. Submedian carinae of first sternum diverging posteriorly, distance separating carinae posteriorly equal to length of first sternum plus fused intercoxal sternite. Legs: Legs without apparent modifications. Flight

wings: Fully developed. Spermatheca: Fig. 14 (male unknown).

*Habitat*.—The holotype was collected among rootlets along the shallow, slightly sandy margin of the clear stream as it tumbled over the polished granite bedrock. The stream was partially shaded, 3 m wide, with a maximum depth of ca. 50 cm; pH, 5.0; oxygen, 12 ppm; hardness, 0; velocity, 46 cm/sec; water temperature, 25°C; and air temperature, 33°C at the time of collection.

*Etymology*.—This new species is dedicated to Armand d'Orchymont in recogni-

tion of his contributions to the systematic literature of the family Hydraenidae.

### Phylogenetic Relationships of the Genus *Adelphydraena*

#### Synapotypic Characters of the Subtribe Hydraenina

All members of the subtribe Hydraenina share two distinctive derived characters: the prosternal intercoxal process is expanded laterally behind the procoxae, closing the procoxal cavities, and the second article of the maxillary palpus is elongate and slender (Perkins 1981: 415, Fig. 148 C; 431). Members of *Adelphydraena* also have these apotypic characters (Figs. 5, 12), and are, therefore, members of the Hydraenina.

#### Synapotypic Characters of *Hydraena* s.l.

In addition to possessing the apotypic characters of the subtribe Hydraenina, members of *Hydraena* s.l. have the following, previously undiscussed, synapotypic characters of the labrum, mandibles, and mentum.

All members of *Hydraena* s.l. have the labrum abruptly widened, slightly depressed and thickened near the base. Each mandible has a dorsolateral process which, when the mandible is closed, fits tightly against and over the widened area of the labrum (fig. 7). The labral and mandibular structures function together to form an interlocking device. Interlocking may, in addition to adding rigidity to the labrum, result in better integration of movement of the labrum and mandibles during feeding and/or function to transfer to the labrum some of the opening and closing power of the strong mandibular muscles.

In all members of *Hydraena* s.l. the mentum has a prominent apicomedian process (Fig. 8). This process is generally lobate in profile and directed obliquely toward the dorsal surface of the head. When the head is seen in dorsal aspect the process is visible

because of the large median emargination between the lobes of the labrum.

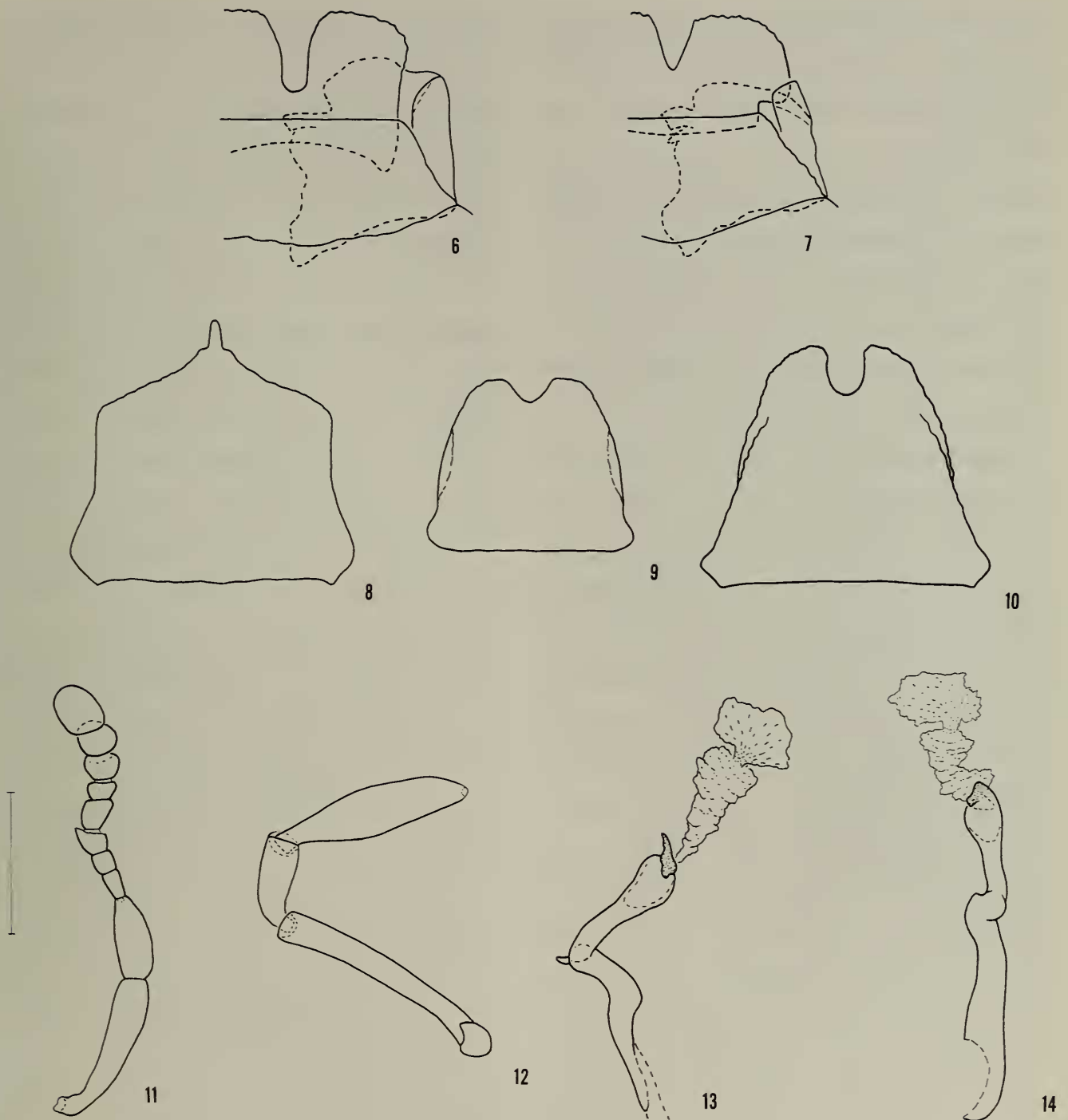
### Synapotypic and Plesiotypic Characters of *Adelphydraena*

The derived characters of the labrum, mandibles, and mentum present in *Hydraena* s.l. are absent in members of *Adelphydraena*. The labrum is straight sided, and the mandible lacks the anteriorly projecting dorsolateral process (Fig. 6). The mentum is emarginate apicomediaally (Figs. 9, 10); this probably represents a derived condition, but in a direction opposite that taken in the lineage leading to *Hydraena*. The apicomedian emargination of the mentum relates to other modifications in the labium; these labial structures will be described and compared with other genera in a separate paper.

The ancestral number of antennal articles for the family Hydraenidae is almost certainly eleven (by outgroup comparison with other Coleoptera). Members of *Adelphydraena* have ten articles (Fig. 11), whereas members of *Hydraena* s.l. represent a further derived step in reduction, having nine articles.

The ancestral number of elytral striae for the order Coleoptera is almost certainly ten (Crowson 1981:42), as is also true for the family Hydraenidae. Members of *Adelphydraena* have the reduced condition of nine complete striae, with stria ten reduced to a few basal punctures (Fig. 1). The elytra of all members of *Hydraena* s.l. show at least some increase in the number of striae (see below). The reduced striae of *Adelphydraena* members is a distinctive dorsal apotypic character.

The prosternal intercoxal process of *Adelphydraena* is unique among Hydraenina in the possession of a longitudinal ridge on each side which extends posteriorly from the median margin of the procoxal cavity. The middle portion of the postcoxal process, between the ridges, is flat or slightly



Figs. 6–14. 6, *Adelphydraena orchymonti*, labrum, mandible, and anterior region of head; 7, *Hydraena riparia* Kugelann, same. 8, *H. riparia*, mentum; 9, *A. orchymonti*, mentum; 10, *A. spangleri*, mentum; 11, *A. spangleri*, antenna; 12, *A. orchymonti*, maxillary palpus; 13, *A. spangleri*, spermatheca; 14, *A. orchymonti*, spermatheca. (Scale line equals 0.1 mm.)

concave, and contiguous with the flat intercoxal area (Fig. 5). In members of *Hydraena* the postcoxal process is raised in the middle, varying from slightly rounded to strongly, longitudinally carinate.

In members of *Hydraena* the proepisternum is emarginate anteriorly, the emargi-

nation providing a ventral opening to the pocket in which the antenna is held (cf. Perkins 1981, figs. 63F, 148C). This emargination is a synapotypic character for the genus *Hydraena*; variation in degree of development of the episternal emargination will be discussed in a separate paper. Mem-

bers of *Adelphydraena* retain the plesiotypic condition, having the proepisternum non-emarginate anteriorly, hence the well developed antennal pockets are not open ventrally (Fig. 5).

Nonpubescent, smooth and shiny submedian areas of the metasternum, termed plaques, are characteristic for the genus *Hydraena*, and frequently provide species-specific characters. The presence of plaques in *Adelphydraena spangleri* (large) and *A. orchymonti* (small) (Figs. 2, 3), suggests that plaques were present in the common ancestor of *Hydraena* and *Adelphydraena*.

In all other Hydraenidae, a portion of the true second sternum is visible between the metacoxae. This can be referred to as the intercoxal sternite (Perkins 1981:21). The intercoxal sternite takes many shapes in the family, but is always separated from the first complete sternum (true third) by a suture. In members of *Adelphydraena* the intercoxal sternite and the first complete sternum are fused, on the same plane, and together form a plate. This plate is delimited on each side by a raised line which originates near the lateral margin of the intercoxal area, and extends diagonally across the first sternum (Figs. 2, 3). In *A. spangleri* the suture between the intercoxal sternite and the first sternum is visible through the cuticle (temporary slide mount), but no surface manifestation of the suture was detected, whereas the suture is visible externally in *A. orchymonti*. Additionally, in both species the first sternum is more tightly joined to the metasternum than is usually seen in members of *Hydraena*, adding to the rigidity of the area surrounding the metacoxae. The discal plate of the first sternum, which is similar to structures found in the family Elmidae, is a distinctive ventral apotypic character.

#### Phylogenetic Relationships within the Genus *Hydraena*

*Hydraena* is a large genus found on all continents. It is quite diverse, and has many

clusters of obviously closely related species. Various, apparently monophyletic, subgroups of *Hydraena* were given formal, subgeneric status by Rey (1886) and Kuwert (1888). Of these subgenera, d'Orchymont (1936) recognized only *Hydraena* s.s., *Haenydra* Rey, and Kuwert's *Phothohydraena*, *Holcohydraena*, and *Taenhydraena*. Perkins (1981:61) compared American *Hydraena* with these subgenera and found that the characters upon which Kuwert's subgenera *Holcohydraena* and *Taenhydraena* were based appeared in only some members of separate monophyletic clusters of species, and concluded that *Holcohydraena* and *Taenhydraena* were not valid. Species with the strial configuration found in members of *Haenydra* and *Phothohydraena* are not known from the New World (Perkins 1981).

In contrast to the views of d'Orchymont (1936) and Perkins (1981), Ienistea (1968, 1978, 1982) considered the subgenera of Rey and Kuwert worthy of full generic status.

In a revealing paper, Berthélemy (1986) compared the elytral striae of several species (principally Palearctic) representing the main groups of *Hydraena* s.l. Using ten striae as the ancestral condition (by outgroup comparison), Berthélemy reasoned that all species with a duplication of striae resulting in the maximum configuration of 3a4b4c2d2e (a-e being nervures), are monophyletic and were derived after the divergence of species with less duplication. Since *Hydraena riparia* Kugelann has this strial configuration, and is the type-species of *Hydraena*, Berthélemy concludes, correctly I think, that all species with the derived condition of 3,4,4,2,2 are rightly members of *Hydraena* s.s.

Perkins (1981:212) erected the genus *Spanglerina* for four species of Central American hydraenines. These four species share several unusual, derived characters, but also have the 3,4,4,2,2 strial configuration. If the nonduplicated condition is considered ancestral for *Hydraena*, and if one assumes that strial duplications have



not been independently derived in different lineages, then one would conclude that the common ancestor of these four species must have arisen within *Hydraena* s.s. *Spanglerina*, therefore, cannot be considered a taxon of equal rank with *Hydraena*, and perhaps for the time being can be treated as a subgenus until the elytra and other structures of the diverse genus *Hydraena* are more completely known.

The strial configurations illustrated by Berthélemy (1986) are summarized below, where the number of striae between the nervures are given for 16 species. Also included are six hypothetical intermediates, each indicated by a (?). Species having primarily two striae between nervures, but with some areas with three punctures, are assigned a value of 2+. Similarly, a value of 3- indicates that there are primarily three striae between the nervures, but with some areas having two punctures.

2	2	2+	2	2	-- gracilis, truncata, bicuspidata, polita
2	2	2+	2-	2-	-- minutissima
2	2	2+	1	2-	-- sharpi
2	2+	2+	1	2	-- ?
2+	2+	2+	2	2	-- ?
2+	2+	3-	1	2	-- pygmaea
2+	2+	3	1	2	-- servilia
2+	3	3	2	2	-- ?
3-	3-	3-	1	2	-- pulchella
3	3-	3-	2-	2	-- stussineri
3	3	3	1	2	-- testacea
3	3	3+	2	2	-- ?
3	3+	3+	2	2	-- ?
3	3+	4	2	2	-- ?
3	4	3	2	2	-- rugosa (reversal)
3	4	4	2	2	-- exarata, quadricollis
3	4	4	2	2+	-- riparia, brachymera

No species illustrated by Berthélemy has the ancestral condition of ten simple striae with no indication whatsoever of duplication. Species traditionally placed in the subgenus *Haenydra* (*gracilis*, etc.) have the least amount of strial duplication, with duplication limited to a portion of stria six. Species sometimes placed in the subgenus *Hadrenya* also have this configuration. Species in

*Hydraena* s.s. have the greatest amount of duplication.

The clinical progression seen in the elytral data can be interpreted as reflecting many phylogenetic divergences from the line which eventually resulted in the maximum expression of strial duplication now known (3,4,4,2,2+). Although further study may reveal that some of the transitional configurations are actually reversals from a more derived condition (Berthélemy 1986), for the sake of discussion we can assume that transitional configurations did exist in some species (or are present in as yet undiscovered ones). This position would be consistent with the uncontested transformational nature of some extant configurations.

Although Berthélemy concludes that striae 2 through 6 are duplicated in *Hydraena* s.s., it would seem that in any instance where there is a whole number increase without intermediate steps known (for example the increase from 3 to 4 striae between nervures a and b, and the similar increase between nervures b and c) we do not know for certain which of the striae became duplicated. But when transitional numbers exist, we can assume that they truly represent retention of the ancestral elytral condition for the monophyletic group of which they are a part, and from their configuration infer which stria was duplicated to form the next higher whole number configuration. For example, it is from the partial duplication of stria 6 present in *gracilis* (etc.), *minutissima* and *sharpi* that we infer that the extra stria between nervures b and c in *testacea* derives from stria 6 rather than stria 5.

With respect to reversions, Berthélemy suggests that perhaps the *pulchella-pygmaea* configuration (2+,2+,3-,1,2) is a reversion from the *Hydraena* s.s. configuration (3,4,4,2,2). However, this would skip the intermediate configuration of 3,3,3,1,2. *H. testacea* has this configuration and also shares with *pulchella-pygmaea* the derived state of only one stria between nervures c and d. According to the subgeneric divisions

recognized by Berthélemy, the strial reduction from two to one between nervures c and d occurred independently in at least three separate lineages.

Based on retention of the presumed ancestral elytral configuration of *Hydraena* s.l., Berthélemy recognizes *Haenydra* as a valid subgenus. He also recognizes *Hadrenya*, although its members have the same configuration as *Haenydra*. This decision is apparently based on the lack of known derived characters shared by all species in these two groups. Similarly, Berthélemy recognizes as valid the subgenus *Phothohydraena*, the members of which have a 3,3,3,2,2 configuration (e.g. *testacea*).

Therefore, formal subgeneric ranking is based upon two criteria: (1) elytra with less duplication than the maximum number (<3,4,4,2,2) and (2) absence of any synapomorphy with species which have the same elytral configuration. If these criteria are accepted, then every species found to have a truly intermediate strial configuration (i.e., not resulting from reversals) and no clear synapomorphy with members of the recognized subgenera, would be treated as representing a new subgenus.

Interestingly, the formal categories of subgenera as now recognized in *Hydraena* are therefore not simply monophyletic clusters of species which are easily recognized (the "sorting categories" of taxonomists), nor do they meet the criteria of sister-groups.

#### Evolution of the Lineage Leading to *Hydraena* s.s.

Based on the apotypic characters discussed above, it can be said that in the subtribe Hydraenina, the following structural modifications were among those that evolved in the lineage leading to *Hydraena* s.s.:

1. Postcoxal process of prosternum develops lateral extensions, closing procoxal cavities

- Antenna becomes reduced from ten to nine articles
  - Labrum-mandible interlocking structure develops
  - Mental apicomedian process develops
  - Proepisternal anterior emargination develops
6. Elytral strial duplications develop

We can be fairly certain that modification of the postcoxal process was the first of these innovations in the Hydraenina because members of *Adelphydraena* have this structure but retain the primitive condition for the antennae, labrum, mandibles, and proepisterna. These four characters are thought to be truly plesiotypic in *Adelphydraena* and not a result of reversals from a derived condition. The following considerations seem to support this position: (A) Reduction in number of antennomeres has occurred in several lineages in the family, but no instance of increase in number of antennomeres is known (Perkins, unpublished). (B) The labrum-mandible interlocking structure is complex, involving corresponding modifications to each structure. The form of the labrum and mandibles in *Adelphydraena* do not suggest reversal from the derived condition.

The mentum of *Adelphydraena*, based upon comparison with other genera (Perkins, unpublished), probably does not represent the ancestral condition for the Hydraenina. The form of the mentum is derived in both genera, but in opposite directions, the apical area being enlarged in *Hydraena* and emarginate in *Adelphydraena*.

The primitive number of elytral striae for the Hydraenina is 10. In *Adelphydraena* none of the striae show any degree of duplication, and stria 10 is reduced to an anterior remnant consisting of a few punctures; consequently, there are only nine complete rows. In known *Hydraena* there is always some degree of strial duplication, and no species show a loss of stria 10.

Of the six structural modifications, the duplication of elytral striae is almost certainly the most recent development. All members of *Hydraena* have the first five derived characters but some members retain the ancestral condition for the striae (except stria six). Further, a transformation series of increasing stria duplication is seen in extant species of *Hydraena*.

The sequence of appearance of the four other structural modifications, if indeed they developed sequentially and not concurrently, is problematic. If they did develop sequentially, their relative positions along the phylogenetic line leading to *Hydraena* s.s. can only be resolved with the discovery of as yet unknown taxa which have more of these derived states than *Adelphydraena*, and less than *Hydraena*.

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- U.S. Dept. of Agriculture, APHIS, Suite 518, 10 Causeway Street, Boston, Massachusetts 02222.